

THE GENERA OF THELYPODIEAE  
(CRUCIFERAE; BRASSICACEAE) IN THE  
SOUTHEASTERN UNITED STATES<sup>1, 2</sup>

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THELYPODIEAE Prantl in Engler & Prantl, Nat. Pflanzenfam. III.  
2: 155. 1891.

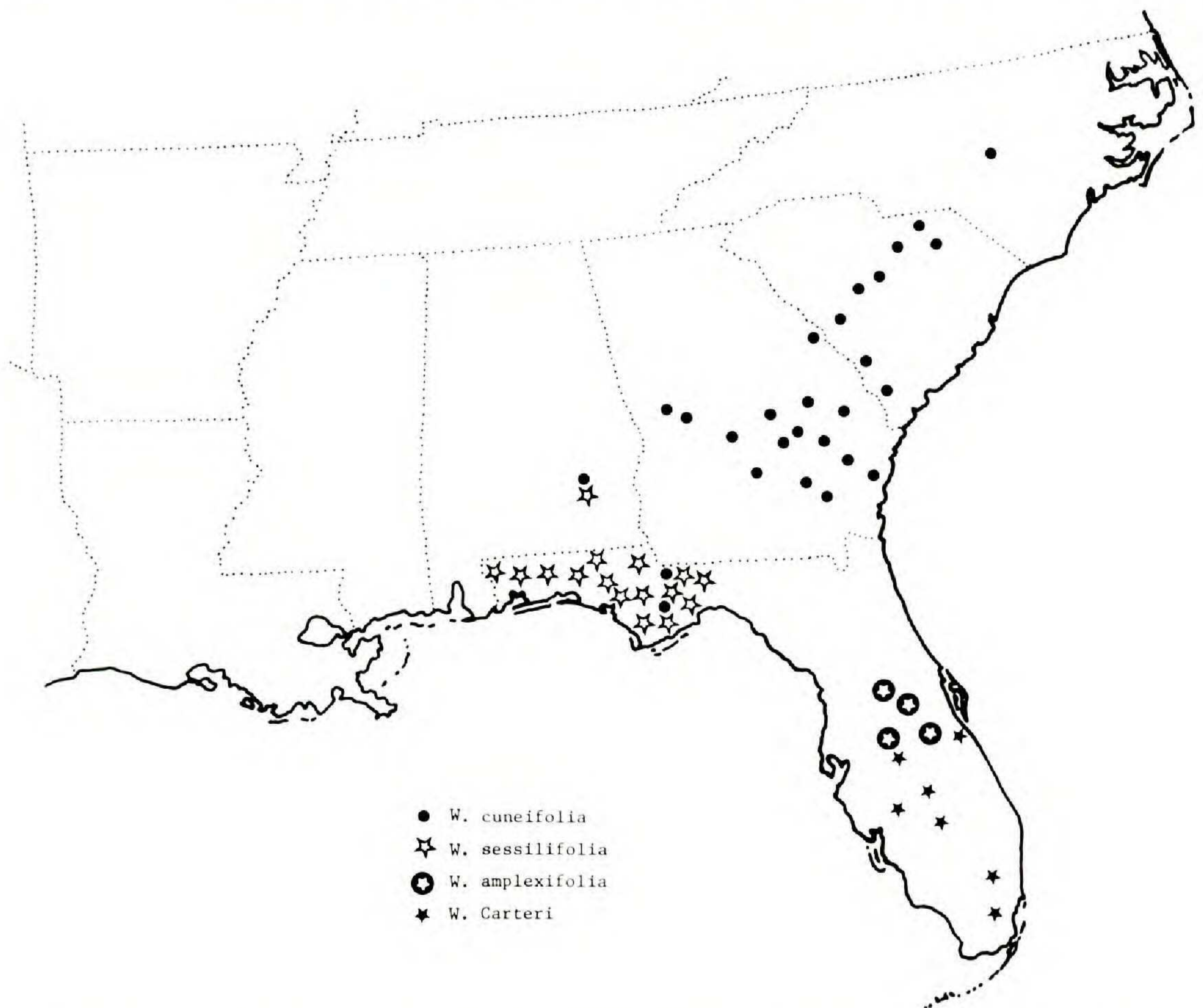
Herbaceous annuals [biennials, or perennials, very rarely shrubs], glabrous or with simple trichomes only [very rarely with furcate hairs]. Inflorescence a terminal raceme or corymb, laxly or densely flowered, often ebracteate. Sepals equal at base (infrequently strongly saccate), erect or spreading, rarely reflexed [or sometimes forming an urceolate, flask-shaped, or slightly bilabiate calyx]. Petals often differentiated into claw and blade [occasionally undifferentiated or attenuate to a clawlike base], usually crisped or channeled. Stamens long-exserted, sometimes slightly protruding [rarely included], equal in length or slightly tetradynamous, rarely in 3 pairs of unequal length; anthers often sagittate at base, linear [or occasionally oblong or ovate], usually coiling circinately after dehiscence; filaments not appendaged, free, or the median ones connate in pairs. Siliques dehiscent, linear, several to many times longer than broad, flattened parallel to the septum [or terete], often borne on a distinct gynophore, rarely sessile. Styles obsolete or evident in fruit. Stigmas entire or slightly [to strongly] 2-lobed; lobes opposite the valves [or replum] in fruit. Seeds winged or wingless, not mucilaginous when wet; cotyledons accumbent [or incumbent]. Base chromosome numbers 10, 11, 12, 13, 14, 15. (Including *Stanleyeae* Rob-

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<sup>2</sup>For an account of the family and its tribes, see I. A. Al-Shehbaz, The tribes of Cruciferae (Brassicaceae) in the southeastern United States. Jour. Arnold Arb. 65: 343–373. 1984.



The nine Southeastern States, showing distributions of species of *Warea*. Each symbol represents a county record.

inson, *Romanschulzieae* O. E. Schulz, *Streptantheae* O. E. Schulz.) TYPE GENUS: *Thelypodium* Endl.

A natural tribe of 11 genera and some 110 species, distributed primarily in North America from the Pacific States eastward to a line extending from North Dakota to Texas, occurring in all the Southeastern States except Tennessee and Mississippi, and from Mexico to Panama, but most numerous in California, Nevada, and Utah, where more than 60 species occur. *Macropodium* R. Br. (two species; Japan, Mongolia, and Siberia) is the only member of the tribe distributed outside North America. Nearly all of the typically tropical representatives of the Thelypodieae belong to *Romanschulzia* O. E. Schulz, the 14 species of which are found mainly at altitudes of 1200–3500 meters (4000–11,500 feet) in wet forests of Mexico (Nuevo León to Oaxaca), Guatemala, Costa Rica, and Panama. The tribe is represented in the southeastern United States by seven indigenous species of *Streptanthus* Nutt. and *Warea* Nutt. The latter is the only endemic genus of Cruciferae in our area (see MAP).

Members of the Thelypodieae can easily be distinguished from those of other tribes by a combination of the following characters: anthers usually exerted, sagittate at base, often linear, usually coiled after dehiscence; filaments equal

in length, sometimes in 3 unequal pairs, or slightly tetradynamous; gynophore present, usually more than 1 mm long; petals crisped or channeled, usually with a distinct claw; and plants glabrous or with simple trichomes.

On the basis of similarities in floral morphology (particularly the presence of a gynophore, exerted stamens of equal length, obsolete styles, spreading parts, and equal sepals) and in several aspects of the fruit (dehiscent, 2-valved, much longer than broad, and many seeded), many authors have postulated that the subfamily Cleomoideae (Capparaceae) is the direct progenitor of the Cruciferae through the intermediate link Thelypodieae. The palynological evidence (Al-Shehbaz, 1973), however, does not support such a direct connection, and it is more likely that the two families evolved from a common ancestor. Any assumptions regarding the ties between the two families must account for members of the Thelypodieae. Some genera of the tribe undoubtedly possess characters more primitive than those found elsewhere in the family, but it is not entirely clear how the Thelypodieae relate to the rest of the Cruciferae. A few authors (Cronquist; Dvořák, 1973) have suggested that the most primitive extant Cruciferae probably occur in central Asia, an assumption apparently lacking a solid morphological foundation and most likely influenced by the hypothesis that the center of greatest taxon diversity and generic endemism represents the center of origin. The assumption has been based primarily on the presence of multicellular glands in some species of *Cleome* L. and the occurrence of their morphological equivalents in some genera of the Hesperideae. Glandular papillae are found on the inflorescences of all species of *Warea*, but whether or not these are anatomically similar to those of *Cleome* remains to be determined. Relict genera of the family are found throughout the world, but almost all of those listed by Hedge are undoubtedly advanced.

Except for two pairs of genera of Thelypodieae, the others are all morphologically well defined and can easily be separated by several characters. *Thelypodium* is very close to *Thelypodopsis* Rydb. and is distinguished primarily by its entire stigmas (two-lobed in the latter genus). The boundaries between *Streptanthus* and *Caulanthus* S. Watson overlap, and the two are separable by a few characters that are sometimes continuous (see the treatment of *Streptanthus*). The relationships among members of the tribe have recently been studied by Hauser and Crovello (1982), who used phenetic and cladistic analyses. Their conclusions coincide in many ways with those reached earlier by Al-Shehbaz (1973), who defined the limits of the tribe primarily on the basis of the nearest sister relatives of its component genera.

Chromosome numbers have been reported for 46 species in nine genera (see Rollins, 1966; Rollins & Rüdénberg). The most common base number is 14, found in *Caulanthus*, *Stanleya* Nutt., *Streptanthella* Rydb., and *Streptanthus*. Other genera have  $x = 10, 11, 12, 13$  (*Thelypodium*), and 15 (*Macropodium*). No cytological data are available for *Romanschulzia* or for *Chlorocrambe* Rydb., a monotypic genus endemic to Oregon and Utah.

The great diversity in floral morphology found among members of the Thelypodieae is not paralleled in any other tribe of the Cruciferae. Floral characters are very useful in distinguishing most of the genera. Although a wide range of variation in the shape, orientation, size, and color of floral parts can occasionally

be found within some genera (e.g., *Streptanthus* and *Thelypodium*), unfortunately very little is known about the floral biology of either these genera or the rest of the tribe.

Nearly all of the Thelypodieae are herbaceous. A woody habit is known only in *Romanschulzia apetala* Rollins, a shrub to 3 m tall endemic to Costa Rica, and in *Stanleya pinnata* (Pursh) Britton, a subshrub of the western United States. Wood anatomy of the latter species was studied by Carlquist, who suggested that the woody habit may have evolved as an adaptation to warmer regions with long growing seasons.

Except for *Caulanthus lasiophyllus* (Hooker & Arnott) Payson and *Streptanthella longirostris* (S. Watson) Rydb., both of which have become weedy in the Pacific and Mountain states and in northern Mexico (Rollins, 1981), the tribe has no economic importance.

#### REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65**: 343–373. 1984), see AVETISIAN (1983), BUSCH, CARLQUIST, CRONQUIST, DVOŘÁK (1971, 1973), GILG & MUSCHLER, HAYEK, HEDGE, JANCHEN, PRANTL, ROLLINS (1966, 1981), ROLLINS & RÜDENBERG (1971, 1977, 1979), SCHULZ, and VILLANI.

AL-SHEHBAZ, I. A. The biosystematics of the genus *Thelypodium* (Cruciferae). Contr. Gray Herb. **204**: 3–148. 1973. [Generic limits and evolutionary trends within the Thelypodieae; pollen of selected Capparaceae.]

———. *Rollinsia*, a new genus of Cruciferae from Mexico. Taxon **31**: 421, 422. 1982.

———. The tribes of Cruciferae (Brassicaceae) in the southeastern United States. Jour. Arnold Arb. **65**: 343–373. 1984.

HAUSER, L. A. Quantitative phylogenetic and phytogeographic studies in the Thelypodieae (Brassicaceae). viii + 260 pp. Unpubl. Ph.D. Thesis, Univ. Notre Dame, Indiana. 1982.

———. Phylogenetic relationships and phenetic similarities among species of *Thelypodopsis* and *Thelypodium* (Brassicaceae). (Abstr.) Am. Jour. Bot. **70**(5, part 2): 116. 1983.

———. Systematic studies in the genus *Stanleya* (Brassicaceae). (Abstr.) *Ibid.* **71**(5, part 2): 170. 1984.

——— & T. J. CROVELLO. Phylogeny, character trends, and distribution patterns in the Thelypodieae tribe (Brassicaceae). (Abstr.) Bot. Soc. Am. Misc. Ser. **160**: 69. 1981.

——— & ———. Numerical analysis of generic relationships in Thelypodieae (Brassicaceae). Syst. Bot. **7**: 249–268. 1982. [Phenetic and cladistic analyses.]

KRAL, R. A report on some rare, threatened, or endangered forest-related vascular plants of the South. U. S. Dep. Agr. Forest Serv. South. Reg. Tech. Publ. R8-TP2. Vol. 1. x + 718 pp. 1983. [*Streptanthus squamiformis*, 528–532; *Warea amplexifolia*, *W. Carteri*, and *W. sessilifolia*, 533–544; descriptions, habitats, maps.]

LICHVAR, R. W. Evaluation of varieties in *Stanleya pinnata* (Cruciferae). Great Basin Nat. **43**: 684–686. 1983. [Reduces *S. pinnata* var. *gibberosa* to synonymy under *S. pinnata* var. *bipinnata*.]

MUSCHLER, R. Cruciferae Andinae. Bot. Jahrb. **40**: 267–277. 1908. [Describes four species of *Thelypodium* and *Streptanthus* from Bolivia and Peru; these are presently assigned to other genera; see AL-SHEHBAZ (1973), GILG & MUSCHLER.]

PAYSON, E. B. Species of *Sisymbrium* native to America north of Mexico. Univ. Wyoming Publ. **1**: 1–27. 1922. [Treatment of 11 species; transferred to *Thelypodopsis* and *Schoenocrambe*; see Rollins, 1982.]

———. A monographic study of *Thelypodium* and its immediate allies. Ann. Missouri

- Bot. Gard. **9**: 233–324. 1923. [*Caulanthus*, *Chlorocrambe*, *Stanleyella*, *Streptanthella*, *Thelypodium*, *Warea*.]
- RAVEN, P. H., & D. I. AXELROD. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. **72**. vi + 134 pp. + 2 pls. 1978. [Thelypodieae, 30.]
- ROBINSON, B. L. Cruciferae. Pp. 98–180 in A. GRAY & S. WATSON, Synoptical flora of North America. Vol. 1. 1895. [Thelypodieae (listed as Stanleyeae), 105, 167–180.]
- ROLLINS, R. C. The cruciferous genus *Stanleya*. Lloydia **2**: 109–127. 1939. [Origin of Cruciferae from Capparaceae-Cleomoideae, 110–112.]
- . A tentative revision of the genus *Romanschulzia*. Contr. Dudley Herb. **3**: 217–226. 1942. [Suggests that *Romanschulzia* be placed with *Thelypodium* in same tribe rather than in a unigeneric tribe.]
- . Some new primitive Mexican Cruciferae. Rhodora **58**: 148–157. 1956. [Comments on *Romanschulzia* and descriptions of three new species.]
- . Miscellaneous Cruciferae of Mexico and western Texas. *Ibid.* **59**: 61–71. 1957.
- . Some sisymbriums (Cruciferae) native to Texas and northeastern Mexico. *Ibid.* **62**: 55–60. 1960. [Four species presently assigned to *Thelypodopsis*; see ROLLINS, 1982.]
- . Studies on Mexican Cruciferae. Contr. Gray Herb. **206**: 3–18. 1976. [*Thelypodopsis* and *Thelypodium*, 11–17.]
- . *Thelypodopsis* and *Schoenocrambe* (Cruciferae). *Ibid.* **212**: 71–102. 1982. [Recognizes 16 species in *Thelypodopsis* and four in *Schoenocrambe*.]
- . Studies on Mexican Cruciferae II. *Ibid.* **214**: 19–27. 1984. [*Romanschulzia Correllii*, *R. Rzedowskii*, and *Thelypodopsis Breedloveii*, spp. nov.]
- RYDBERG, P. A. Studies on the Rocky Mountain flora—XVIII. Bull. Torrey Bot. Club **34**: 417–437. 1907. [Discussion of *Thelypodium*, key, and original descriptions of the segregates *Thelypodopsis*, *Pleurophragma*, *Hesperidanthus*, *Stanleyella*, *Heterothrix*, and *Chlorocrambe*, 428–436.]
- WELSH, S. L., & N. D. ATWOOD. An undescribed species of *Thelypodopsis* (Brassicaceae) from the Uinta Basin, Utah. Great Basin Nat. **37**: 95, 96. 1977. [*T. argillacea*, sp. nov.; transferred by Rollins (1982) to *Schoenocrambe*.]

KEY TO THE GENERA OF THELYPODIEAE IN THE  
SOUTHEASTERN UNITED STATES

- Sepals reflexed, rarely spreading; floral buds clavate or pyriform; gynophore slender, (3–) 5–14 mm long; petal claws slender, papillose or pubescent; stamens equal in length; fruiting pedicels deciduous from the rachis, often leaving elevated scars; seeds striate, wingless. . . . . 1. *Warea*.
- Sepals erect or ascending; floral buds oval or lanceolate; gynophore stout, 1–2(–4) mm long; petal claws broad, flat, glabrous; stamens slightly tetradynamous or in 3 pairs of unequal length; fruiting pedicels persistent; seeds minutely reticulate, winged. . . . . 2. *Streptanthus*.

1. **Warea** Nuttall, Jour. Acad. Nat. Sci. Phila. **7**: 83. 1834.

Glabrous and occasionally glaucous annual herbs; stems slender, often branching above, leafless below. Lowermost leaves undescribed; middle and upper ones entire, short-petiolate or sessile. Inflorescence a short, ebracteate, corymbiform, terminal raceme, slightly elongating in fruit. Pedicels slender, sometimes filiform, straight, with 2 lateral, gland-tipped papillae at the base. Floral buds clavate or pyriform. Sepals linear to spatulate, not saccate at base, strongly reflexed and subappressed to pedicel, rarely widely spreading, green or same color as petals. Petals spreading, white, pink, or deep purple, clawed;

blades orbicular or obovate, equal or rarely slightly unequal, often abruptly narrowed to claw, sometimes cuneate or attenuate at base; claws minutely papillose to conspicuously pubescent, often slightly dilated at base. Glandular tissue subtending bases of all stamens, usually developed into 6 teeth alternating with filaments, the 4 teeth adjacent to the lateral stamens larger than the 2 alternating with the median ones. Stamens spreading, long-exserted, equal in length; filaments filiform, glabrous, often slightly dilated at base; anthers linear, sagittate at base, usually coiling circinately when fully dehisced. Ovary borne on a long gynophore; style obsolete; stigma entire. Fruiting pedicels often deciduous from the infructescence axis, usually leaving elevated, disclike scars. Siliques dehiscent, narrowly linear, glabrous, flattened parallel to the septum, horizontal or reflexed, straight or arcuate; valves with a prominent midnerve extending full length; gynophores slender, (3–)5–14 mm long. Seeds uniseriately arranged, wingless, brown, longitudinally striate, not mucilaginous when wet; cotyledons accumbent. TYPE SPECIES: *Stanleya amplexifolia* Nutt. = *W. amplexifolia* (Nutt.) Nutt.; see Payson, 1923. (Name commemorating Nathaniel A. Ware, 1789–1853, a teacher in South Carolina who traveled widely in the southeastern United States.)

A very well-defined genus of four species endemic to the southeastern United States in North and South Carolina, Georgia, Alabama, and Florida (see MAP). Species of *Warea* are restricted to the southeastern Coastal Plain, where they grow primarily on sandy soils in pinelands, dry open *Quercus* woods or scrub, and sandhills. Flowering and fruiting generally occur in the spring and summer, but under favorable conditions successive generations of a given species may be produced throughout the year. All four species are morphologically and geographically distinct. No infrageneric subdivisions are recognized.

The most widely distributed species of the genus is *Warea cuneifolia* (Muhl.) Nutt. (*Cleome cuneifolia* Muhl., *Stanleya gracilis* DC.), which occurs in certain counties of Florida (Liberty and Gadsden), Alabama (Pike), Georgia (Talbot, Ben Hill, Pierce, Montgomery, Richmond, Long, Taylor, Pulaski, Laurens, Wheeler, Bacon, Emanuel, Bulloch, Tattnall, and McIntosh), South Carolina (Jasper, Allendale, Aiken, Lexington, Richland, Kershaw, Darlington, and Chesterfield), and North Carolina (Harnett). The nearest relative of *W. cuneifolia* is *W. Carteri* Small,  $2n = 24$ , which is endemic to southern peninsular Florida (Brevard, Polk, Highlands, De Soto, Glades, Broward, and Dade counties). Both species have short-petiolate, cuneate, oblanceolate, or linear leaves and white flowers. The former is characterized by its glabrous or minutely papillose petal claws and by gynophores that are longer than the fruiting pedicels; the latter is easily recognized by its densely pubescent or somewhat fimbriate claws and by gynophores that are shorter than the fruiting pedicels. A few authors (e.g., Patman) have reduced *W. Carteri* to synonymy under *W. cuneifolia*, but such action is totally unwarranted, as is evidenced by the distinctive morphology and distribution of the two species.

*Warea amplexifolia* (Nutt.) Nutt. (*Stanleya amplexifolia* Nutt., *W. auriculata* Shinnars) is a rare species confined to central peninsular Florida (Lake, Orange, Polk, and Osceola counties). It differs from the other species of *Warea*

in having deeply auriculate and amplexicaul, ovate to lanceolate or oblong cauline leaves. Flower color is generally white changing to light purple.

*Warea sessilifolia* Nash is similar to *W. amplexifolia* in having sessile, ovate or lanceolate cauline leaves, but the leaves are not amplexicaul and are without auricles (or are rarely minutely auriculate), and the flowers are dark purple. It is distributed throughout the panhandle of Florida (from Leon and Wakulla counties westward through Escambia County) and in Alabama (Pike County). All reports of *W. amplexifolia* from areas outside central peninsular Florida are based on misidentifications of plants of *W. sessilifolia*.

Nuttall's original description of *Stanleya amplexifolia* was based on a fruiting specimen collected by Nathaniel Ware from "east" Florida (actually the central peninsular area). He transferred this species in 1834 to his new genus *Warea* after acquiring flowering material from "west" Florida (the panhandle area). Nuttall did not realize that he was dealing with two distinct entities, and that the flowering material and its illustration, which accompanied the original description of the genus, clearly belong to a different species (described later by Nash as *W. sessilifolia*). Without studying any of Nuttall's specimens, Shinnery mishandled the nomenclature of both species, believing that Nuttall made a mistake in the locality (east vs. west), that both the flowering and fruiting specimens were collected from West Florida, and that Nuttall did not have a mixture of two species. Shinnery reduced *W. sessilifolia* to synonymy under *W. amplexifolia* and redescribed the plants of central peninsular Florida as *W. auriculata*. (See Channell & James for further details.)

*Warea* is very well defined morphologically and is apparently without immediate relatives among the Thelypodieae. Both *Stanleya* Nutt. and *Romanschulzia* O. E. Schulz resemble it in several aspects of the flowers and fruits, but no close ties are found between any two of these genera (see Hauser & Crovello). Furthermore, it is highly unlikely that *Warea* is ancestral to *Streptanthus* Nutt., as was suggested by Hayek. The characters that in combination easily distinguish *Warea* from the other genera of the Cruciferae are corymbose inflorescences, clavate buds, spreading floral parts, slender and papillate or pubescent petal claws, long-exserted stamens of equal length, long gynophores, striate seeds, and fruiting pedicels that are deciduous from the rachis (see Al-Shehbaz, 1984, fig. 2, a, b).

Hardly anything is known about the chemistry, embryology, anatomy, genetics, or ecology of *Warea*. Chromosome counts ( $n = 12$ ,  $2n = 24$ ) for *W. Carteri* are known from a single collection (Rollins & Rüdénberg, 1977). The adaptive value and the phylogenetic significance of the glandular papillae found in the inflorescence of all species of *Warea* are unknown. With the exception of *W. cuneifolia*, the species of the genus are listed as endangered or threatened in Florida and Alabama.

The genus has no economic value. *Warea sessilifolia* has very showy inflorescences and might well be used as an ornamental.

#### REFERENCES:

Under family references in AL-SHEHBAZ (Jour. Arnold Arb. 65: 343-373. 1984), see HAYEK, PATMAN, RADFORD *et al.*, RICKETT, ROLLINS & RÜDENBERG (1977), SCHULZ, and

- SMALL. Under tribal references see AL-SHEHBAZ (1973), HAUSER & CROVELLO (1982), KRAL, PAYSON (1923), and ROBINSON.
- AHLES, H. E., C. R. BELL, & A. E. RADFORD. Species new to the flora of North or South Carolina. *Rhodora* **60**: 10–32. 1958. [*W. cuneifolia* from Harnett County, North Carolina, 16.]
- AYENSU, E. S., & R. A. DEFILIPPS. Endangered and threatened plants of the United States. xv + 403 pp. Washington, D. C. 1978. [*W. amplexifolia* and *W. Carteri* endangered in Florida, *W. sessilifolia* threatened in Alabama and Florida.]
- CHANNELL, R. B., & C. W. JAMES. Nomenclatural and taxonomic corrections in *Warea* (Cruciferae). *Rhodora* **66**: 18–26. 1964. [Excellent account of the historical background of nomenclatural discrepancies in *Warea*, key to species, distributions; see SHINNERS, SMALL (1896).]
- DEAN, B. E., A. MASON, & J. L. THOMAS. Wild flowers of Alabama and adjoining states. xxii + 230 pp. University, Alabama. 1973. [*W. cuneifolia* and *W. sessilifolia*, 72, 73.]
- DUNCAN, W. H., & L. E. FOOTE. Wild flowers of the southeastern United States. vii + 296 pp. Athens, Georgia. 1975. [*Warea*, colored photo of *W. sessilifolia* (not *W. cuneifolia*, as stated), 50.]
- FREEMAN, J. D., A. S. CAUSEY, J. W. SHORT, & R. R. HAYNES. Endangered, threatened, and special concern plants of Alabama. 25 pp. Auburn, Alabama. 1979. [*W. sessilifolia*, threatened, reported from Pike County, 12, fig. 28; *W. amplexifolia*, a misidentification of the former species, 25.]
- HARPER, R. M. The “pocosin” of Pike County, Alabama, and its bearing on certain problems of succession. *Bull. Torrey Bot. Club* **41**: 209–220. 1914. [*W. cuneifolia*, addition to the state flora, 212; record needs verification.]
- . A preliminary list of the endemic flowering plants of Florida. *Quart. Jour. Florida Acad. Sci.* **12**: 1–9. 1950. [*W. amplexifolia* and *W. sessilifolia*, 7, 8.]
- KRAL, R. Some notes on the flora of the Southern States, particularly Alabama and middle Tennessee. *Rhodora* **75**: 366–410. 1973. [First record of *W. sessilifolia* from Alabama, listed as a synonym of *W. amplexifolia*, 389.]
- LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of vascular plants of Collier, Dade, and Monroe counties, Florida. *Bot. Lab. Univ. S. Florida Contr.* **15**. viii + 95 pp. Coral Gables, Florida. 1965. [*W. Carteri* (listed as *W. cuneifolia*) in Dade County, 41.]
- LONG, R. W., & O. LAKELA. A flora of tropical Florida. xvii + 962 pp. Coral Gables, Florida. 1971. [*Warea*, 432; suggestion that *W. Carteri* may be conspecific with *W. cuneifolia*.]
- NASH, G. V. Notes on some Florida plants.—II. *Bull. Torrey Bot. Club* **23**: 95–108. 1896. [*W. sessilifolia*, sp. nov., 101.]
- NUTTALL, T. A description of some of the rarer or little known plants indigenous to the United States, from the dried specimens in the herbarium of the Academy of Natural Sciences in Philadelphia. *Jour. Acad. Nat. Sci. Phila.* **7**: 61–115. *pl. 10*. 1834. [*Warea*, 83–85; *Warea* and *Stanleya* represent a natural “order” intermediate between the Cruciferae and Capparaceae.]
- ROLLINS, R. C. The need for care in choosing lectotypes. *Taxon* **21**: 635–637. 1972. [Comments on Shinners’s mishandling of the typification of *W. amplexifolia*; see SHINNERS.]
- SHINNERS, L. H. *Warea auriculata* instead of *W. amplexifolia* of Small (Cruciferae). *Sida* **1**: 105, 106. 1962. [Misinterpretation of Nuttall’s material upon which *W. amplexifolia* was originally based; see CHANNELL & JAMES, ROLLINS.]
- SMALL, J. K. Studies in the botany of the southeastern United States—VII. *Bull. Torrey Bot. Club* **23**: 405–410. 1896. [*Warea*, 408, 409; see CHANNELL & JAMES.]
- . Additions to the flora of peninsular Florida. I. Native species. *Ibid.* **36**: 159–164. 1909. [*W. Carteri*, sp. nov., 159, 160.]



WUNDERLIN, R. P. Guide to the vascular plants of central Florida. 472 pp. Tampa and other cities, Florida. 1982. [*Warea*, 195.]

2. **Streptanthus** Nuttall, Jour. Acad. Nat. Sci. Phila. 5: 134. 1825.

Annual [biennial or perennial], often glaucous, glabrous or sparsely [to densely] hispid [or hirsute], taprooted herbs. Basal and lowermost cauline leaves usually absent in flowering specimens [rarely forming a definite rosette], petiolate or sessile, thin [sometimes coriaceous or somewhat fleshy], dentate or pinnatifid to pinnatisect [runcinate or divided into linear or filiform segments]. Upper cauline leaves usually sessile, amplexicaul [or auriculate], sometimes short- [or long-]petiolate, linear, lanceolate, ovate, oblong [or of other shapes], entire or dentate. Inflorescence an ebracteate [very rarely bracteate], dense or lax, many- [or few-]flowered raceme [or panicle]; rachis straight [rarely flexuous], elongating in fruit; flowering pedicels ascending, divaricate, or reflexed [rarely secund]. Flowers actinomorphic or slightly [to strongly] zygomorphic, all fertile [occasionally the terminal cluster of flowers sterile, having larger and showier sepals than those of the fertile ones, and with other floral parts aborted or lacking]. Calyx regular [or irregular], campanulate, subcylindrical [or usually flask shaped, somewhat bilabiate, or urceolate], open [or closed] at apex; sepals equal or unequal at base, all or only the inner pair saccate, lanceolate to oblong [ovate or rarely orbicular], erect or ascending, separate [or connivent], herbaceous [or somewhat fleshy or membranaceous], acute or obtuse, cucullate [or not] at apex, usually scarious at margin, with straight or recurved tips, purple or green [white, yellow, red, or purplish black], glabrous or sparsely to densely hairy or setose [rarely with a subapical tuft of stiff hairs], round [or prominently keeled], uniform in size [or the adaxial (upper) sepal smaller than or markedly larger than and subtending the other 3]. Corolla cruciform, usually becoming slightly [to strongly] bilabiate by the divergence of petals in opposite pairs; petals always strongly differentiated into blade and claw, equal in size, shape, and color [or the adaxial pair smaller than or much larger than the abaxial one, or differing in color and/or shape], lavender or light to dark purple or magenta [green, yellow, white, brown, red, or purplish black]; blades broadly obovate, 2–4 times wider than the claw, or linear to oblanceolate or oblong [or spatulate] and as broad as or narrower than the claw, entire or partly [to wholly] undulate or crisped, usually reflexed, uniformly colored or with the center and/or veins darker; claws included, spatulate or oblanceolate, crisped, usually channeled. Stamens equal in length, somewhat tetradynamous, or in 3 unequal pairs (with the adaxial pair usually the longest), exerted to slightly protruding, or the outer pair [or all] included; filaments free, or those of 1 (the adaxial) or both median pairs partially to completely connate, straight or recurved; anthers linear or oblong, apiculate or obtuse, sagittate at base, all polliniferous, or those of the adaxial pair of stamens abortive and much shorter than the others. Glandular tissue flat, subtending the bases of all or only the lateral stamens. Siliques narrowly [to broadly] linear, somewhat [to very strongly] flattened parallel to the septum [very rarely subterete], 1–7 mm wide, smooth [or torulose], erect, divaricate [or pendent];

valves obscurely [to prominently] 1-nerved from base to apex, glabrous [hispid or setose]; style short or obsolete in fruit; stigma entire or 2-lobed, the lobes always opposite the valves; gynophore short [rarely exceeding 4 mm]; septum somewhat thick [or membranaceous and translucent]. Seeds oblong to orbicular, not mucilaginous when wet, usually minutely reticulate [or nearly smooth], brown, winged [rarely wingless]; wing narrow [or to 1–1.5 mm wide], completely surrounding the seed [or restricted to the distal end]; funiculus free or partially [to completely] adnate to the septum, slender or flattened; cotyledons accumbent or obliquely so. Base chromosome number 14. (Including *Agianthus* Greene, *Cartiera* Greene, *Disaccanthus* Greene, *Euklisia* (Nutt. ex Torrey & Gray) Rydb. ex Small, 1903 (*Euclisia* (Nutt. ex Torrey & Gray) Greene, 1904), *Icianthus* Greene, *Mesoreanthus* Greene, *Microsemia* Greene, *Mitophyllum* Greene, *Pleiocardia* Greene.) TYPE SPECIES: *S. maculatus* Nutt. (Name from Greek, *streptas*, twisted, and *anthos*, flower, in reference to the petals.) — TWIST-FLOWER, JEWEL FLOWER.

A genus of about 35 species in three subgenera and probably more than seven sections, distributed from Louisiana and Arkansas westward through Kansas and all the southwestern United States, the Mountain States (except Montana), and the Pacific States (except Washington), as well as in northern Mexico (Baja California, Chihuahua, and Coahuila). The great majority of the species (26) occur in California, and 14 of these are found in the western part of the state, particularly in the counties of the Coast Ranges north and south of San Francisco Bay. A few other species are endemic to the serpentine outcrops of the Sierra Nevada foothills from Shasta County to Fresno County. *Streptanthus cordatus* Nutt. is distributed in all the Mountain and Pacific states except Washington and Montana. Five species are endemic or primarily restricted to south-central or western Texas (Big Bend National Park and surrounding counties); one, *S. platycarpus* Gray, is localized in northern Mexico, and another, *S. carinatus* Wright, is widely distributed in New Mexico and Arizona. *Streptanthus* is represented in the southeastern United States by three species distributed in southwestern Arkansas and northwestern Louisiana, as well as in adjacent Texas, Oklahoma, and Kansas.

Infrageneric groups in *Streptanthus* have not been satisfactorily treated; formal sectional classification has been published only for subgenus EUCLISIA Nutt. ex Torrey & Gray (Kruckeberg & Morrison). Rodman and colleagues provided an informal provisional nomenclatural synopsis of *Streptanthus* in which they followed Jepson in reducing *Caulanthus* to two subgenera of *Streptanthus*. However, several authors (see Rollins, 1971; Al-Shehbaz; Rollins & Holmgren) have clearly demonstrated that, in order to obtain a workable classification in this group, both genera must be recognized. Strongly diverging from Jepson's position, Schulz recognized 11 genera (including *Caulanthus*) in this complex and retained only three species in *Streptanthus*. In this he followed Greene's splitting of the genus into nine segregates that are largely based on minor differences in the flower. Neither Schulz's nor Jepson's opposing generic concepts are practical, and they cannot be accepted.

Two species of *Streptanthus* occurring in the Southeast belong to subgenus

STREPTANTHUS (*Eustreptanthus* Endl.), a group of six or seven species distributed in Texas and its neighboring states and in northern Mexico. Plants of this subgenus are characterized by having petal blades usually broadly obovate and often more than twice the width of the claw; stamens free, tetradynamous or in three unequal pairs, with the anthers all fertile; stigmas strongly 2-lobed; siliques (2-)4-7 mm wide; flowers actinomorphic, rarely zygomorphic; and calyx usually regular, open at the apex. No sections have been proposed in subgenus STREPTANTHUS, but it is clear that at least two or probably three can be recognized.

*Streptanthus maculatus* Nutt. (*S. obtusifolius* Hooker, *Brassica Washitana* Muhl., *Stanleya Washitana* (Muhl.) DC.) is confined to rocky bluffs and moist woodlands in northeastern Texas, southeastern Oklahoma (McCurtain and Pushmataha counties), and southwestern and central Arkansas (Pike, Montgomery, Garland, Hot Springs, Saline, and Pulaski counties). With its broadly obovate, reflexed, purple petals of equal size, each with a central magenta spot, its glabrous and purplish sepals, its ovate or oblong, amplexicaul cauline leaves, and its divaricately ascending siliques that are 6-10 cm long and 2-2.5 mm wide, this is the most attractive and one of the most distinctive species in the genus.

A very close relative and a member of the same subgenus, *Streptanthus squamiformis* Goodman is endemic on sandstone and soft shale in *Pinus-Quercus-Carya* forests (see Kral for further details) of southeastern Oklahoma (McCurtain County) and southwestern Arkansas (Polk, Howard, and Sevier counties). The remarkable similarities between the two species in every respect except the pubescence and the sepals may support considering them as conspecific. The pedicels and sepals in *S. squamiformis* are characteristically pubescent with trichomes that are 1-2 mm long, thick, widely spreading, and (upon drying) scalelike; the sepals are generally long-cucullate. In *S. maculatus* the sepals are glabrous and not cucullate (or with only the outer pair bearing short cuculli). There is some variation in the amount of pubescence and in the thickness of trichomes on the sepals and pedicels of *S. squamiformis*, but in the absence of any field studies and crossing experiments between this and *S. maculatus*, the two are best treated as distinct species.

*Streptanthus hyacinthoides* Hooker (*Icianthus hyacinthoides* (Hooker) Greene, *Euklisia hyacinthoides* (Hooker) Small, *S. glabrifolius* Buckley, *I. glabrifolius* (Buckley) Greene) grows primarily on sand in *Pinus*, *Quercus*, or *Carya* woods, open areas, roadsides, grassy sandhills, and sand dunes in northwestern Louisiana (Winn, Caddo, and Bienville parishes), southwestern Arkansas (Nevada and Ouachita counties), eastern Texas, central and northwestern Oklahoma, and adjacent Kansas (Barber and Comanche counties). The linear-lanceolate, short-petiolate or sessile cauline leaves, the pendent or horizontally spreading, deep-purple or magenta (rarely lavender) flowers, the open calyx, and the fused median filaments with aborted adaxial anthers serve to distinguish this species from all the others of the genus.

The subgeneric disposition of *Streptanthus hyacinthoides* is problematic. Earlier authors such as Gray and Watson (1871) placed it in subgenus EUCLISIA Nutt. ex Torrey & Gray, while Rodman and associates assigned it to subgenus

**STREPTANTHUS.** Subgenus **EUCLISIA** is characterized by zygomorphic flowers; reduced petal blades as wide as or narrower than the claw; three unequal pairs of stamens with the filaments of one or both pairs of the median stamens partially to completely connate; anthers of the upper (adaxial) stamens sterile; entire (rarely 2-lobed) stigmas; and narrow siliques 1–2 mm wide. All of these features are found in *S. hyacinthoides*, and they clearly support its placement in subgenus **EUCLISIA**. However, it clearly deviates from the 14 species of this subgenus, which are exclusively Californian and primarily serpentine endemics, by its open calyx that is regular and neither flask shaped nor urceolate. From members of subgenus **STREPTANTHUS**, *S. hyacinthoides* differs in having entire stigmas, narrow petal blades, connate median filaments, sterile adaxial anthers, and narrow siliques. Greene (1906a), who was the first to point out the differences between the typical members of *Euclisia* and *S. hyacinthoides*, proposed *Icianthus* to accommodate the species. Perhaps the best disposition for this species would be in a monotypic section, not yet proposed, of subgenus **EUCLISIA**.

Subgenus **PLEIOCARDIA** (Greene) Jepson, not represented in our area and primarily distributed in California, accommodates the remaining species of the genus. Members have slightly zygomorphic flowers, three usually unequal, free pairs of stamens with all anthers fertile, usually entire stigmas, and narrow petal blades often as wide as the claw.

The genera most closely related to *Streptanthus* are *Streptanthella* Rydb. and *Caulanthus* S. Watson. From these, *Streptanthus* is distinguished by its accumbent cotyledons, usually winged seeds, and flattened siliques. *Caulanthus* species usually have incumbent cotyledons, wingless seeds, and terete fruits. The line separating the last two genera, however, is not as well defined as it may seem, and there are few species that could be accommodated in either genus without drastically altering the generic limits. Nevertheless, a more practical taxonomy of the group can be achieved by maintaining both genera. Many other pairs of closely related genera with equally arbitrary boundaries are found in the Cruciferae. The monotypic *Streptanthella* is separated from *Streptanthus* by its incumbent cotyledons and its beaked siliques in which the valves remain undehisced in the beak area. Hauser and Crovello suggested that these two genera probably evolved from *Caulanthus*.

Several species of *Streptanthus* are highly polymorphic in flower color and pubescence. The most notable example is *S. glandulosus* Hooker, which has an enormous array of morphologically discrete forms that are apparently correlated with the spatial isolation of populations. As many as nine species have been described in this complex, but these were shown to be interfertile (Kruckeberg, 1957, 1958). Because of the importance of the flowers in the taxonomy of the genus, careful field notes should be made, particularly with respect to color, degree of irregularity, and petal size and orientation.

The remarkable diversity of the flowers of *Streptanthus* is certainly unparalleled in any genus of the Cruciferae. The specific epithets of *S. hyacinthoides* and *S. polygaloides* are indicative of the strong superficial resemblance of the flowers of these plants to those of the genera *Hyacinthus* L. (Liliaceae) and

*Polygala* L. (Polygalaceae). As shown in the generic description above, the calyx and corolla vary greatly in color, shape, size, orientation of parts, and symmetry. The androecium, too, is highly evolved and shows a wide range of variability, particularly with respect to the length, color, orientation, and degree of connation of the median stamens, and the fertility or sterility of the adaxial anthers. These patterns undoubtedly represent adaptations to certain pollinators, about which hardly anything is known. Kruckeberg (1957) observed bees, butterflies, beetles, and even hummingbirds visiting the flowers of *S. glandulosus*, but no attempt was made to identify the species of these pollinators.

Self-incompatibility and protandry were demonstrated in *Streptanthus carinatus* and *S. Cutleri* Cory (Rollins, 1963). In both species flower odor reaches its peak during anther dehiscence, while nectar secretion coincides with the maturation of the gynoecium. Both devices are nicely coordinated to fulfill the requirements for insect attraction. Selfing is reduced or prevented in many taxa of subgenus EUCLISIA by protandry and the curvature of the filaments away from the stigma during full anthesis. Data on the reproductive biology of the majority of species are needed.

A uniform haploid chromosome number of 14 has been reported for at least 18 species (Kruckeberg, 1958; Rollins, 1966; Rollins & Rüdénberg, 1977; Kruckeberg & Morrison). Earlier counts of  $n = 12$  for *Streptanthus cordatus* may have been in error, or the species may have a deviant chromosomal race. No chromosome counts are available for the three species occurring in our area.

Extensive hybridization experiments have been conducted within sections EUCLISIA, INSIGNES Kruckeberg & Morrison, and HESPERIDES Kruckeberg & Morrison. In all cases species of a given section can be crossed, but the artificial hybrids either are inviable or suffer from reduced pollen fertility (Kruckeberg, 1957; Kruckeberg & Morrison). No visible meiotic irregularities during microsporogenesis were observed that explain the low degree of pollen viability. Natural hybridization in *Streptanthus* was first reported between two subspecies of *S. carinatus* (Kruckeberg *et al.*).

Forty species of *Streptanthus* and *Caulanthus* have been analyzed for their seed glucosinolates, and 26 compounds have been identified (Rodman *et al.*). In general, the glucosinolate profiles have been shown to be species specific, but the two genera are chemically indistinguishable. The serpentine endemics are apparently as complex and diverse in their glucosinolates as the nonserpentine taxa. Although infraspecific variability in these compounds is significant in six species, only *S. cordatus* shows a clear correlation, with morphological discontinuities corresponding to recognizable infraspecific taxa. Seeds of *S. hyacinthoides* contain two volatile compounds (3-butenyl as the major component and allyl glucosinolate in smaller concentrations) and two non-volatiles, with 4-methylsulfinylbutyl as the major constituent and 2-hydroxy-3-butenyl glucosinolate as the minor. *Streptanthus maculatus* (listed as *S. orbicularis*), by contrast, contains two volatiles, with allyl glucosinolate as the dominant constituent and 3-butenyl glucosinolate as the minor one.

Of the 32 species of *Streptanthus* and *Caulanthus* analyzed for nickel content

(Reeves *et al.*), *S. polygaloides* is the first known hyperaccumulator in the New World, with values in the range of 3300–14,800 parts per million of dry weight. Other serpentine-tolerant species had nickel values of only 10–100 ppm. Greene (1904) established the monotypic genus *Microsemia* for this species on the basis of its very broad, bannerlike, adaxial sepal that subtends the other sepals in bud, a feature not encountered elsewhere in the Cruciferae. The nickel data may support Greene's position, but in floral and fruit morphology the species fits well in *Streptanthus*.

Edaphic factors probably play a major role in the localized distribution of most species of *Streptanthus*. Although many species are restricted to limestone, shale, sand, clay, and granite gravel and rocks, by far the narrowest endemism is shown by the serpentine inhabitants. Kruckeberg's pioneering studies on serpentine tolerance show that some species (such as *S. glandulosus*, *S. tortuosus* Kellogg, and *S. cordatus*) are broad generalists adapted to different soils, while others (at least 22 taxa of 15 species) are serpentine endemics. Ecotypic differentiation in the form of several serpentine-tolerant and intolerant races is now well documented in *S. glandulosus*. Kruckeberg believes that evolutionary diversification in *Streptanthus* may have resulted from the reduced gene flow between edaphic races accentuated by spatial and edaphic isolation, particularly in serpentine habitats, and that the serpentinophytes probably represent the end product of a process of biotype depletion in which the serpentine intolerants were eliminated by competition pressure, leaving only the serpentine obligates.

#### REFERENCES:

- Under family references in AL-SHEHBAZ (Jour. Arnold Arb. **65**: 343–373. 1984), see HAYEK, ROLLINS (1966), ROLLINS & RÜDENBERG (1977), and SCHULZ. Under tribal references see AL-SHEHBAZ (1973), HAUSER & CROVELLO (1982), KRAL, MUSCHLER, RAVEN & AXELROD, and ROBINSON.
- BROOKS, R. E., R. L. MCGREGOR, & L. A. HAUSER. Vascular plants new to the state of Kansas. Tech. Publ. State Biol. Surv. Kansas **1**: 1–12. 1976. [*S. hyacinthoides* in Comanche and Barber counties, 4.]
- BROWN, C. A. Wildflowers of Louisiana and adjoining states. xl + 247 pp. Baton Rouge, Louisiana. 1972. [*S. hyacinthoides* growing on deep sand in Winn Parish, 59.]
- CORY, V. L. A new *Streptanthus* from the Big Bend of Texas. *Rhodora* **45**: 258–260. 1943. [*S. Cutleri*, sp. nov.]
- GOODMAN, G. J. A new species of *Streptanthus*. *Ibid.* **58**: 354, 355. 1956. [*S. squamiformis*, sp. nov., from Oklahoma and Arkansas.]
- GRAY, A. On *Streptanthus*, Nutt., and the plants which have been referred to that genus. *Proc. Am. Acad. Arts Sci.* **6**: 182–188. 1864. [Two subgenera recognized: *Eustreptanthus*, three species, and *Euclisia*, 13 species.]
- GREENE, E. L. Certain West American Cruciferae. *Leafl. Bot. Obs. Crit.* **1**: 81–90. 1904. [*Euclisia*, *Pleiocardia*, *Mitophyllum*, *Microsemia*, and *Mesoreanthus* segregated from *Streptanthus*.]
- . *Icianthus* and *Sprengeria*. *Ibid.* 197–199. 1906a.
- . Four streptanthoid genera. *Ibid.* 224–229. 1906b. [*Disaccanthus*, *Cartiera*, *Guillemia*, and *Agianthus* segregated from *Streptanthus* and *Thelypodium*.]
- HERMANN, F. J. Notes on western range forbs: Cruciferae through Compositae. U. S.

- Dep. Agr. Forest Serv. Agr. Handb. **293**: 1–365. 1966. [*S. tortuosus* said to be palatable to sheep, 17.]
- HOFFMAN, F. W. Studies in *Streptanthus*. A new *Streptanthus* complex in California. *Madroño* **11**: 189–220. 1952. [Key to the subgenera of *Streptanthus* (including *Caulanthus*); key to the groups of section *Euclisia*; *S. Morrisonii* and *S. brachiatus*, spp. nov.]
- HOOKE, W. J. *Streptanthus obtusifolius*. Blunt-leaved streptanthus. *Bot. Mag.* **61**: pl. 3317. 1834.
- . *Streptanthus hyacinthoides*. Hyacinth-flowered streptanthus. *Ibid.* **63**: pl. 3516. 1836.
- HOWELL, J. T. The Tompkins-Tehipite expedition of the California Academy of Sciences. *Leaflet West. Bot.* **9**: 181–187. 1961. [*S. fenestratus*, key to related species, 184, 185.]
- . A new variety of *Streptanthus cordatus*. *Ibid.* **10**: 31. 1963.
- . The juvenile leaves of a California jewel flower. *Ibid.* 135, 136. 1964. [*S. polygaloides*.]
- . A new Sierran *Streptanthus*. *Ibid.* 182, 183. 1965. [*S. Farnsworthianus*, sp. nov.]
- JEPSON, W. L. A flora of California. Vol. 2. *Frontisp.* + 684 pp. Berkeley. 1936. [Recognizes 25 species in four subgenera of *Streptanthus*, *Caulanthus* reduced to two subgenera, 20–35.]
- KRUCKEBERG, A. R. Intraspecific variability in the response of certain native plant species to serpentine soil. *Am. Jour. Bot.* **38**: 408–419. 1951. [Response of *S. glandulosus* strains to serpentine and nonserpentine soils, the role of biotype depletion in the origin of serpentine endemics.]
- . The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* **35**: 267–274. 1954. [Tolerance and intolerance to serpentine among strains of *S. glandulosus*.]
- . Variation in fertility of hybrids between isolated populations of the serpentine species, *Streptanthus glandulosus* Hook. *Evolution* **11**: 185–211. 1957. [Artificial hybridization between members of 32 populations in 334 combinations; interfertility studies support the reduction of the 12 species in the complex to three.]
- . The taxonomy of the species complex, *Streptanthus glandulosus* Hook. *Madroño* **14**: 217–227. 1958. [Interfertility relationships; recognizes *S. glandulosus* (three subspecies and three varieties), *S. albidus* (two subspecies), and *S. niger*.]
- . The implication of ecology for plant systematics. *Taxon* **18**: 92–120. 1969a. [Edaphic specialization of *Streptanthus*, 97, 98.]
- . Soil diversity and the distribution of plants, with examples from western North America. *Madroño* **20**: 129–154. 1969b. [Obligate serpentine endemics of *Streptanthus*, 142.]
- & J. L. MORRISON. New *Streptanthus* taxa (Cruciferae) from California. *Madroño* **30**: 230–244. 1983. [Five new sections in subgenus *Euclisia*; *S. drepanoides*, sp. nov.; *S. insignis* subsp. *Lyonii*, subsp. nov.; crosses among some members of section *Insignes*.]
- , J. E. RODMAN, & R. D. WORTHINGTON. Natural hybridization between *Streptanthus arizonicus* and *S. carinatus* (Cruciferae). *Syst. Bot.* **7**: 291–299. 1982. [First report of natural hybridization in *Streptanthus*; interfertility, karyology, and glucosinolate chemistry support the reduction of *S. arizonicus* to a subspecies of *S. carinatus*.]
- MARTIN, P. S., & C. M. DREW. Scanning electron photomicrographs of Southwestern pollen grains. *Jour. Arizona Acad. Sci.* **5**: 147–176. 1969. [Pollen of *S. arizonicus* is prolate, tricolpate, and with visible columellae, 150, fig. 27B–D.]
- MORRISON, J. L. Studies in the genus *Streptanthus* Nutt. I. Two new species in section *Euclisia* Nutt. *Madroño* **4**: 204–208. 1938. [*S. batrachopus* and *S. callistis*, spp. nov.]

- . A monograph of the section *Euclisia* Nutt., of *Streptanthus* Nutt. Unpubl. Ph.D. Thesis, Univ. California, Berkeley. 1941.\*
- MUNZ, P. A., & D. D. KECK. A California flora. *Frontisp.* + 1681 pp. Berkeley and Los Angeles. 1959. [*Streptanthus*, 216–221.]
- NUTTALL, T. Description of two new genera of the natural order Cruciferae. *Jour. Acad. Nat. Sci. Phila.* **5**: 132–135. 1825. [*Streptanthus*, 134, 135, *pl.* 7.]
- REEVES, R. D., R. R. BROOKS, & R. M. MACFARLANE. Nickel uptake by Californian *Streptanthus* and *Caulanthus* with particular reference to the hyperaccumulator *S. polygaloides* Gray (Brassicaceae). *Am. Jour. Bot.* **68**: 708–712. 1981.
- RODMAN, J. E., & A. R. KRUCKEBERG. Patterns of seed glucosinolate variation in the genus *Streptanthus* (Cruciferae). (Abstr.) *Bot. Soc. Am. Misc. Ser.* **158**: 96. 1980.
- , ———, & I. A. AL-SHEHBAZ. Chemotaxonomic diversity and complexity in seed glucosinolates of *Caulanthus* and *Streptanthus* (Cruciferae). *Syst. Bot.* **6**: 197–222. 1981. [Glucosinolates of 89 collections of 40 species; 26 compounds identified; phenogram of 38 species based on glucosinolate profiles; provisional nomenclatural synopsis of *Streptanthus* (including *Caulanthus*); serpentine taxa are chemically as diverse and complex as nonserpentine ones.]
- ROLLINS, R. C. Some new or noteworthy North American Cruciferae II. *Contr. Dudley Herb.* **3**: 366–373. 1946. [*S. oliganthus*, *sp. nov.*, 372, 373.]
- . Protandry in two species of *Streptanthus* (Cruciferae). *Rhodora* **65**: 45–49. 1963. [Protandry, self-incompatibility, and zygomorphy in *S. Cutleri* and *S. carinatus*.]
- . Notes on *Streptanthus* and *Erysimum* (Cruciferae). *Contr. Gray Herb.* **200**: 190–195. 1970. [*S. sparsiflorus*, *sp. nov.*; key to the species of *Streptanthus* of Texas.]
- . Protogyny in the Cruciferae and notes on *Arabis* and *Caulanthus*. *Ibid.* **201**: 3–10. 1971. [Generic limits of *Streptanthus* and *Caulanthus*; argument for maintaining both genera.]
- & U. C. BANERJEE. Pollens of the Cruciferae. *Publ. Bussey Inst. Harvard Univ.* **1979**: 33–64. 1979. [*S. carinatus*, *S. platycarpus*, and *S. hyacinthoides*; pollen prolate; interspecific differences in the size and abundance of lumina, 48–51.]
- & P. K. HOLMGREN. A new species of *Caulanthus* (Cruciferae) from Nevada. *Brittonia* **32**: 148–151. 1980. [*C. Barnebyi*, *sp. nov.*; a brief comment on maintaining both *Caulanthus* and *Streptanthus*.]
- , E. A. SHAW, & R. J. DAVIS. Cruciferae. Pp. 671–706 in D. S. CORRELL & M. C. JOHNSTON, *Manual of the vascular plants of Texas*. Renner, Texas. 1970. [*Streptanthus*, 676, 677.]
- RYDBERG, P. A. Studies on the Rocky Mountain flora—XVI. *Bull. Torrey Bot. Club* **33**: 137–161. 1906. [The typification and limits of *Euklisia*, 142.]
- SHAPIRO, A. M. Egg-mimics of *Streptanthus* (Cruciferae) deter oviposition by *Pieris sisymbrii* (Lepidoptera: Pieridae). *Oecologia* **48**: 142, 143. 1981. [Orange-pigmented callosities on the leaves of *S. Breweri* and *S. glandulosus* mimic in shape, size, and color the eggs of *P. sisymbrii*; these affect the egg-laying of the insect, which visually assesses the egg load on individual host plants before ovipositing.]
- SJOLUND, R. D., & T. E. WEIER. An ultrastructural study of chloroplast structure and differentiation in tissue cultures of *Streptanthus tortuosus* (Cruciferae). *Am. Jour. Bot.* **58**: 172–181. 1971.
- SMITH, E. B. An atlas and annotated list of the vascular plants of Arkansas. iv + 592 pp. Fayetteville, Arkansas. 1978. [*S. hyacinthoides*, *S. maculatus*, *S. squamiformis*, 135, 136.]
- THIERET, J. W. Twenty-five species of vascular plants new to Louisiana. *Proc. Louisiana Acad. Sci.* **32**: 78–82. 1969. [*S. hyacinthoides* from Bienville and Caddo parishes, 79.]
- TORREY, J., & A. GRAY. A flora of North America. Vol. 1. xiv + 711 pp. New York. 1838–1840. [*Streptanthus*, 75–78 (1838), 666 (1840).]
- WATSON, S. Botany. U. S. Geol. Expl. Fortieth Parallel **5**. liii + 525 pp. + 40 *pls.* 1871. [*Streptanthus*, 19, 430, 431; *Caulanthus*, 27, 28.]



- . Contributions to American botany. 1. Miscellaneous notes upon North American plants, chiefly of the United States, with descriptions of new species. Proc. Am. Acad. Arts Sci. **25**: 124–163. 1890. [*Streptanthus*, grouping of 22 species, 125–127.]

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